THE CRANIUM OF *HADRONOMUS PUCKRIDGI* WOODBURNE, 1967 (MACROPODOIDEA: MACROPODIDAE) A PRIMITIVE MACROPODID KANGAROO FROM THE LATE MIOCENE ALCOOTA FAUNA OF THE NORTHERN TERRITORY

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ABSTRACT

Originally described from its dentition and lower jaw only, the affinity of *Hadronomus* within the Macropodidae had not been resolved. The cranium of *Hadronomus* gives a better understanding of its broader affinity with other kangaroos, although its precise systematic position remains ambiguous with regard to known fossil and living macropodids. On the basis of its cranial wall morphology and its previously described dentition, *Hadronomus* appears to be a member of the Macropodidae that shares predominately plesiomorphic features with the sthenurines. Otherwise, *Hadronomus* is very distinctive in many respects from known macropodines and sthenurines, and it has not been possible to establish a direct relationship with any named anneetant macropodid group. The maxilla and molars of an unassigned mid-Miocene form described by Flannery *et al.* (1982) resemble those of *Hadronomus*, as do some specific features of the lower molars, dentary and incisor of *Galanarla tessellata*, another primitive macropodid of unknown subfamilial affinity. The genus *Hadronomus* appears to be the terminal form of an ancient lineage of macropodids that could represent a sister group of the Sthenurinae.

KEYWORDS: Macropodid cranial morphology, Sthenurinae, late Miocene, macropodid systematics.

INTRODUCTION

Woodburne (1967) concluded from the dentition that *Hadronomus* shows a number of characters "...which are prophetic of Pliocene and Pleistocene protemnodonts and ... late Cenozoic members of the Sthenurinae. Because the late Cenozoic history of the Macropodidae is poorly understood and because temporally and structurally intermediate forms are absent, the animal cannot be assigned to a subfamily." A significant further observation was that considerable morphological change would have had to occur if *Hadronomus* were ancestral to *Sthenurus* and/or *Protemnodon* and finally, that *Hadronomus* "...is better suited as an ancestor to *Sthenurus* than to *Protemnodon*."

While the possible relationships of *Hadronomus* to subsequent later Cenozoic macropodine genera are of great interest, little can be added to Woodburne's observations based

on the dentitions. Some features of the cranium of *Hadronomus* appear to support his opinion that the genus is closer to *Sthenurus* than to *Protemnodon*. On the other hand, *Hadronomus* has many unique characters and character combinations that may have some bearing on the broader question of macropodid-potoroid relationships.

The dentition of *Hadronomus* has been described in detail by Woodburne (1967) and requires no further treatment at this time. Although dentitions of *Hadronomus* are relatively common in the Alcoota Fauna, even fragmentary remains of the cranium are extremely rare. The specimen in this description (NT Museum number ASP889) was recovered during the last few days of our 1988 field season. The context of the specimen was unusual in being found isolated from the typical bone-bed material. The cranium was preserved in poorly consolidated sediment, lying adjacent to the cranium of a pouch

young of *Kolopsis torus*. No other significant remains were recovered from the immediate area.

MATERIALS AND METHODS

ASP889 (*Hadronomus puckridgi*) a partial cranium including right maxilla, palate, jugal, auditory region and a portion of the orbital wall and neurocranium. The dorsal surface of the neurocranium and rostrom is missing, as is most of the premaxilla and its dentition. The specimen is slightly compressed dorsoventrally. The cranium was directly compared with whole and dissected cranial specimens of the extant forms *Aeypyprymnus rufescens*, *Potorous tridactylus*, *Onychogalea unguifera*, *Thylogale billardieri*, and *Macropus* spp.

SYSTEMATICS

The classification of *Hadronomus puckridgi* Woodburne, 1967 follows Aplin and Archer (1987), as follows: Suborder Phalangerida, Superfamily Macropodoidea, Family Macropodidae, Subfamily *Incertae sedis*.

Aplin and Archer (1987) argue for the separation of the Potoroidae and Macropodidae at the familial level. They base their conclusions on the gross morphological differences in female reproductive tracts and spermatozoan morphology of the respective families. They also suggest that there is both biochemical and palaeontological evidence of an early separation of the two families "...perhaps sometime during the Oligocene" (Aplin and Archer 1987). I support Aplin and Archer's conclusion, if not all of their reasoning, because of the enormous sometimes radical diversification within both divisions and the anomalous results of implying equivalent morphological distance between say, the Sthenurinae and the Macropodinae and the Potoroniae and the Macropodinae.

Subfamily *Incertae*
(Figs 1-7)

Hadronomus puckridgi Woodburne, 1967:82-103, figs 14-17.

Revised diagnosis. Low, broad neurocranium with alisphenoid-parietal contact; widest at the level of the glenoid fossae. Zygomatic arch long, straight; jugal strap-like and deep throughout its entire length. Lateral glenoid eminence highly developed. Poorly developed prezygomatic sulcus and short, blunt masseteric processes. Orbital margin thin, sharp; small, deep, elliptical orbital fossa. Masseteric crest on jugal straight, attachment surface of the masseter not expanded anteroventrally towards the masseteric process. Palate with large, posteriorly confluent greater palatine vacuities; diastemal and premaxillary palate, not strongly flexed downwards; shallow, posteriorly tapering suborbital shelf. Low, elongated auditory arch, strongly slanted posteriorly; wide, ventrally thick, cancellous, posterodorsally incomplete ectotympanic, large elliptical auditory meatus. Alisphenoid tympanic wing relatively broad and slightly inflated. Petrous bone elongated, floccular fossa large, oval in outline and shallow with rounded orificial margins. Posterior neurocranium low relative to the occlusal line. Upper cheektooth row slightly curved, upper permanent premolar elongated, sectorial; shearing crest consisting of seven small cusps and bearing a low lingual crest. Upper molars low crowned, simple, bilophodont and lacking ornamentation, lophs thin and trenchant; crowns lengthen anterior to posterior, broad midvalleys widen progressively from front to back, blocked labially by two longitudinal crests (buccal cingulum and postparaconal crest) divided by a sulcus. M_2 with low, wide short anterior midlink and hindling incipiently developed. Postparaconal and premetaconal facets developed at the labial end of the lophs; short paraconal crest and low postparaconal, premetaconal and postmetaconal crests present on all molars; hypoloph of M_5 reduced. I_1 crown lanceolate, lacking enamel on lingual surface, long, nearly straight root; conspicuous, boss-like alveolar crest on dentary above the root of I_1.

Remarks. The cranium of *Hadronomus* appears to fit more comfortably with the Macropodidae than with the Potoroidae on the basis of its molar morphology, neurocranial sutural figuration and the presence of a well developed, cuspule-bearing lingual crest on the upper permanent premolar. The molars are basically similar to those of the Sthenurinae. However, as Woodburne (1967) implies, there are more synapomorphies between the Sthenurinae and the Macropodinae, particularly with the genus *Protemnodon*,
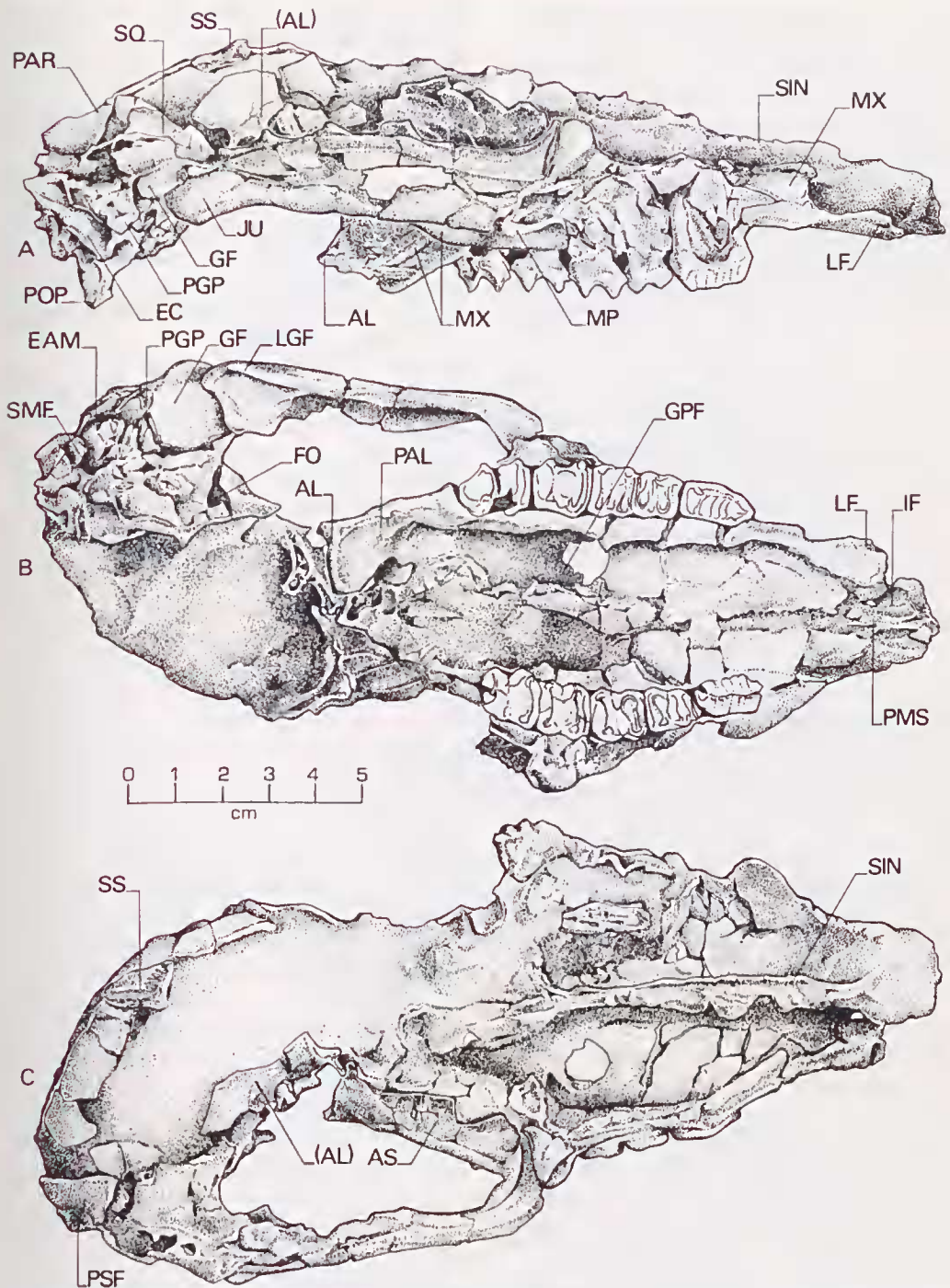
Fig. 1. Line illustration of *Hadronomus puckridgi* Woodburne, 1967: A, note straight, horizontal diastemal palate, long strap-like Jugal and posteriorly low neurocranium in lateral aspect; B, large palatine vacuities, straight profile of zygomatic arch and well-developed lateral glenoid process in lateral aspect; C, long squamosal sulcus, broad rostrum and braincase in dorsal aspect. Abbreviations: **PAR**, parietal; **SQ**, Squamosal; **SS**, sagittal suture; **AL**, position of alisphenoid; **SIN**, choanal septum; **MX**, maxilla; **LF**, lingual foramen or canine alvcolus; **MP**, masseteric process;**AL**, alisphenoid; **JU**, jugal; **GF**, glenoid fossa; **PGP**, postglenoid process; **EC**, ectotympanic; **OP**, paroccipital process; **LGF**, lateral glenoid flange, **EAM**, external auditory meatus; **SMF**, stylomastoid fossa or suleus; **FO**, foramen ovale; **PAL**, palatine; **GPF**, greater palatine fenestra; **IF**, incisive foramen; **PMS**, septal process of the premaxilla; **PSF**, postsquamosal foramen; **AS**, alveolar or suborbital shelf of the maxilla.

than there are between either of those subfamilies and *Hadronomus*. The plesiomorphic condition of the cranium of *Hadronomus* suggests that it is not directly related to either macropodid subfamily, both of which share many synapomorphic features in the zygomatic arch, orbit and neurocranium.

Description and Comparison

General description. The cranium of *Hadronomus* (Figs 1, 2) is significantly larger than any of the largest living macropodid species, being approximately the size of the crania of some *Protemnodon* species (Fig. 1). The neurocranium is low and broad with a triangular outline shape (Fig. 1B,C). The splanchnocranial region is horizontal with only a minimal expression of the sharp downward flexion of the antepremolar maxillary region typical of the majority of macropodines (Fig. 1A). The conspicuously elongated jugal has a flat, as opposed to a bowed contour, and maintains an almost constant depth from beneath the orbit to its flange-like termina-
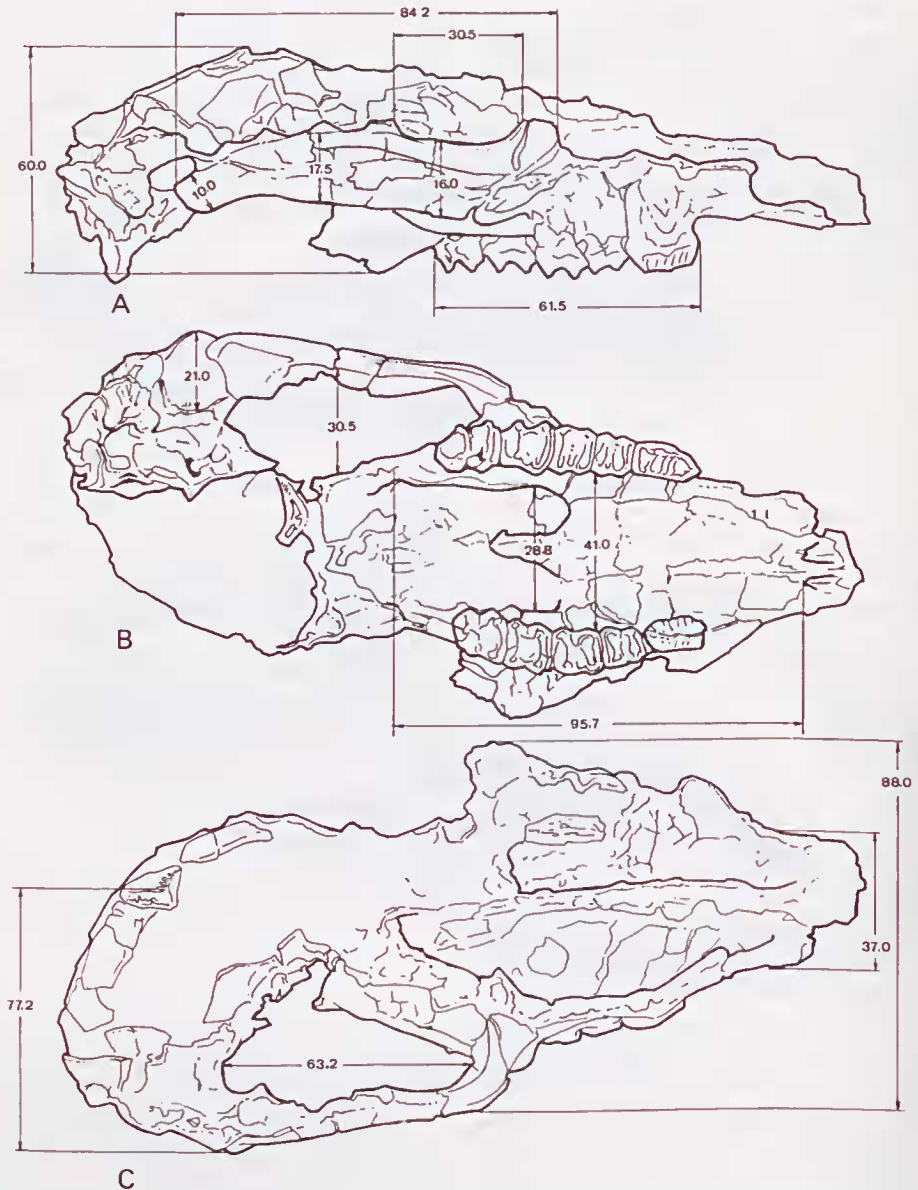

Fig. 2. Measurements (in millimetres) of the cranium of *Hadronomus puckridgi*: **A**, lateral aspect; **B**, ventral aspect; **C**, dorsal aspect.

tion lateral to the glenoid fossa. This contrasts strongly with the majority of living macropodine kangaroos among which the jugal tapers sharply away from the masseteric process. The masseteric process is a short, blunt anteroposteriorly directed crest of the maxilla in which the jugal does not participate. The glenoid fossa is wide, deep and confined laterally by a deep jugal crest and its internal lunette. The postglenoid process is comparatively stout. A remnant of the lambdoid crest indicates that the posterior portion of the neurocranium projected posteriorly over the occiput (Figs 3, 7A). The external auditory meatus is a low and broad aperture occupying most of the large, posteriorly inclined auditory arch.

The palate is broad, flat and relatively shallow to the alveolar margins. The posterior palate is invaded by large, partially divided greater palatine fenestrae. The cheek tooth rows are nearly straight, the curvature of the left cheek tooth row being exaggerated by post-depositional distortion (Fig. 1B). The incisive foramina are located close together on either side of the premaxillary suture. A labial foramen or small canine alveolus is present on the diastemal crest within the premaxillary-maxillary suture. The supradiastemal (buccinator) fossa is shallow. The contour of a remnant of maxilla on the left side (Fig. 1B,C) is similar to that of a Euro which implies that the rostrum was rather inflated immediately above the diastema.

The remnants of the neurocranium indicate that the back of the skull was low and broad. Although the frontal and alisphenoid are poorly preserved, a fragment of the parietal shows the most likely relationship of the sutures (Fig. 3). The alisphenoid takes an oblique anteroposterior course across the lateral wall of the braincase as in typical macropodines, indicating that the frontal did not make contact with the squamosal (Fig. 3). A small triangular fragment on the dorsal midline preserves the frontoparietal contact at the convergence of the frontal and sagittal crests. The trend of the frontoparietal (coronal) suture is acutely anterolateral as in mature *Macropus giganteus* and *Macropus rufa.*

Premaxilla. Although little of the premaxilla is represented, the approximate course of the premaxillary-maxillary suture can be traced from the posterior margins of the inci-

sive foramina, anterolaterally to the diastemal crest. The suture appears to course posteriorly on the lateral surface of the snout immediately above the diastemal margin for about 15.0mm after which it ascends vertically for about 10.0mm then courses obliquely posteriorly. A small canine alveolus or a labial foramen is developed in the suture at the level of the posterior margins of the incisive foramina. The suture defines a short anteriorly directed process of the maxilla which terminates along the posterior margins of the incisive foramina. The incisive foramina are divided by a comparatively large, posteriorly invasive midline process of the premaxilla. The base of the premaxilla follows the same nearly horizontal trend as the maxillary diastema to the point where it is broken. It may be safely assumed that the rest of premaxillary palate also projected straight forward. The lateral profile of the anterior palatal region therefore more closely resembles that of the potoroids *Hypsiprymnodon* and *Potorous* than any of the typical macropodine kangaroos.

Maxilla. The maxillary palate is crushed, though largely intact. The original surface appears to have been shallowly concave posteriorly and flat in the diastemal area. As in potoroids and some primitive macropodines, large greater palatine fenestrae are present. These are long, parallel-sided ovoid vacuities, partially divided by a midline process and are similar in form and extent to those present in sthenurine kangaroos and the macropodine *Dorcopsis* (Figs 1B, 2B). The maxillary roots of both zygomatic arches are present, and by reference to both sides, the entire structure can be restored. In contrast to macropodines, the infraorbital fossa is indistinct and low. The surface of the maxilla immediately anterior to the orbit is convexly confluent with the jugal, rather than forming the long, oblique crest characteristic of macropodine kangaroos. The masseteric process of the maxilla is short, blunt and laterally compressed. Other than the masseteric process, it appears that the maxilla makes no further contribution to the zygomatic arch. Although the sutures are indistinct in this region it seems likely that the jugals extended a considerable distance (>10.0mm) anterior to the orbital margin. The morphology of the maxillary root of the zygomatic arch of *Hadronomus* thus differs from that of typical
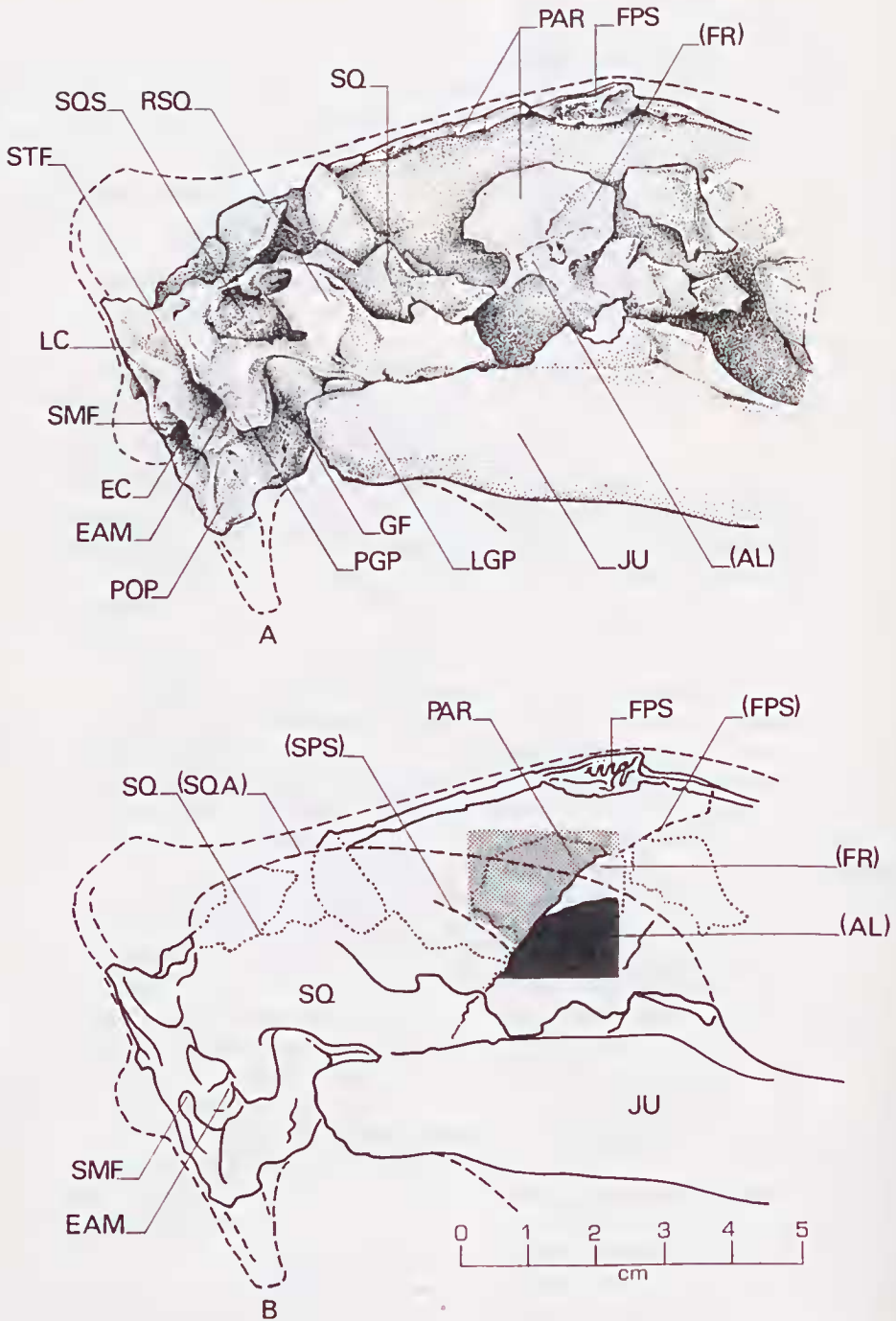
Fig. 3. Lateral aspect of the neurocranium of *Hadronomus puckridgi*; **A**, though badly damaged, the relations of the braincase laminae are preserved; **B**, schematic interpretation of the braincase wall. Additional abbreviations: **SQ**, remnant of squamosal; **SQS**, breached squamosal sinus; **STF**, supratympanic fossa; **LC**, lambdoidal crest; **FPS**, frontoparietal suture; **FPS**, projection of the frontoparietal suture; **FR**, posterior-most position possible of the frontal bone; **SQA**, postulated outline of the missing squamosal portion of the zygomatic arch.

macropodines in having a short, poorly developed anteorbital crest, an indistinct, low infraorbital sulcus and a broad preorbital process of the jugal, in essence a condition intermediate to potoroines and macropodines.

The suborbital shelf of the maxilla is a platform-like structure; wide laterally but shallow dorsoventrally and distinctly tapered posteriorly. It is about half as deep as the equivalent structure in *Macropus rufa* and *Macropus robusta*. The alisphenoid and palatine sutures are poorly defined in the postalveolar region of the shelf, but a long, low, mesially extensive postalveolar process of the maxilla is present (Fig. 1A,B). The infraorbital canal lies at the anterior extremity of a deep oval fossa, the lateral margin of which developes into a distinct, rounded crest forming the dorsal contour of the entire length of the suborbital shelf. The suborbital region of *Hadronomus* is thus quite distinct from that of the larger macropodine kangaroos and resembles somewhat the potoroine condition, in which the shelf strongly tapers off posteriorly. It is however, proportionally deeper than that of *Potorous tridactyus*, more resembling the condition in *Aepyprymnus*. The suborbital sutural morphology is obliterated by numerous cracks and cannot be traced.

Zygomatic arch. A striking feature of *Hadronomus* is its long, straight, strap-like jugal. It differs from that of macropodine kangaroos in maintaining an almost equal width for about two-thirds of its total length (Figs 1, 7). This condition is accentuated by the virtual absence of an anterior jugal eminence and the development posteriorly of a deep lateral glenoid crest with a blunt margin. The dorsal margin of the jugal describes the inferior border of the orbit emarginated behind by a prominent postorbital process; posterior to which the squamosal-jugal contact continues on in a smooth, gently arcing suture. The orbital notch is comparatively shallow giving the impression that the orbit was somewhat more elliptical than the typically round macropodine condition. The masseteric crest is correspondingly long and faithfully follows the dorsal profile for about three-quarters of the length of the bone. In most, if not all macropodine kangaroos, the masseteric line is composed of two distinct arcs or describes a wide V-shape.

A straight, nearly horizontal inscription can be seen on the jugals of *Aepyprymnus*,

although its inferior jugal border strongly tapers toward the glenoid fossa, commencing in line with the base of the postorbital process. The inferior margin of the jugal of *Hadronomus* is relatively much thicker and more rounded in contrast to the thin, tapered margins of the large living macropodines. The jugal of the sthenurine kangaroo, *Sthenurus atlas*, bears a resemblance to that of *Hadronomus* in having a comparatively straight masseteric line.

The lateral glenoid crest or eminence encloses a 5.0mm deep lunate depression that forms the anterolateral portion of the glenoid fossa. Its posteroinferior margin is roughened, presumably for the lateral craniomandibular ligament. The lateral glenoid eminence is present in the larger macropodine and sthenurine kangaroos, but in *Macropus* sp. it is not remotely developed to the extent found in *Hadronomus*. The lateral glenoid eminence is strongly expressed in *Sthenurus (Simosthenurus)* species. From the lateral aspect, the deep, rounded posterior margin of the jugal in *Sthenurus maddocki* appears very similar to that of *Hadronomus*. However, in ventral aspect the fossa is relatively smaller and shallower due to the thick, ventromedially tapering base of the crest. Palorchestines (*Propalorchestes*, *Palorchestes*) are the only other diprotodontans having an equivalent degree of development of this structure. Living potoroids typically lack a lateral glenoid eminence.

The anterior orbital surface of the jugal bears a deep, oval preocular or "lacrimal" fossa situated superolateral to the infraorbital canal opening. In the majority of macropodines this structure is fairly shallow and is often more of a deep, crescentic groove. Although variable in both subfamilies, it tends to be a very deep, ovoid structure in potoroids and therefore similar to that of *Hadronomus*. The position of this fossa within the orbit is also significant in that it is situated in the inferolateral margin of the orbit in macropodines, some distance behind the anteriormost extent of the orbital margin. In potoroids it opens at the anterior extreme of the orbital fossa. With respect to its position, *Hadronomus* is more like the potoroids due to the more anterior extent of the jugal.

The squamosal portion of the zygomatic arch is poorly preserved. The broken edges of the process indicate that it was moderately

deep and relatively long. The squamosal sulcus is very long and less slanted anteroposteriorly than in *Macropus* spp.

The glenoid fossa is wide and flat. The transverse axis of the articular surface is greater relative to its length, although its basic shape does not differ significantly from that of the larger *Macropus* species. The increased transverse width of the fossa is reflected in the marked lateral deviation of the marginal profile of the squamosal adjacent to the fossa. The postglenoid process is large and projects ventrolaterally as opposed to the more or less ventral projection of the structure in living *Macropus*. The combined structures of the lateral glenoid eminence and the large ventrolaterally projecting postglenoid process result in a deep, posterolaterally confined fossa, although its large dimensions and the flat articular surface indicate that the condyle was very mobile, as in other kangaroos. The overall construction of the glenoid region is very similar to that of the Sthenurinae, implying that the dentary condyle of *Hadronomus* was likewise transversely elongated and large.

Neurocranium. The dorsal surface of the neurocranium is not preserved. A portion of the lateral wall of the braincase is present, sufficient to determine the basic sutural configuration (Fig. 3). The thin, overlapping sutural margin of the squamosal lamina is entirely missing and separated from the parietal fragment by a gap about 7.0mm wide. It is likely that the squamosoparietal suture was located near the posterior edge of the parietal fragment, and may have overlapped it a short distance. However, there are no sutural crenulations present on either surface. The anteroinferior surface of the parietal fragment is inscribed with a fine crest which I interpret to be the posterior margin of the alisphenoid and therefore the actual trend of the alisphenoidoparietal suture. The height and angle of this sutural line indicates that the anterior process of the parietal was long and that the course of the frontal towards the squamosal was interrupted by the alisphenoid. A second, almost vertical crest that intersects the alisphenoid crest may represent a faint infratemporal crest or the posterior-most extent of the frontal, which in any case is overlapped by the alisphenoid and does not necessarily indicate that the separation of the squamosal from the frontal was narrow. Given the angle

of the frontoparietal suture projected from the bone fragment conveniently retaining the sagittal-frontal crest confluence, the frontoparietal suture was at an acute angle and coursed a considerable distance anterior to the anterior edge of the squamosal. It can be concluded therefore that the sutural arrangement was like that of the macropodine kangaroos rather than the potoroids. This character is no longer considered to be a consistent feature for differentiating macropodids from potoroids because a recently discovered fossil *Hypsiprymnodon* species has the frontal separated from the squamosal by the alisphenoid (Flannery and Archer 1987a) and this is also the case in *Bettongia moyesi* (Flannery and Archer 1987b). Other examples of this inconsistancy within specific clades are known, for example in the thylacoleonids (Murray *et al.* 1987). In the case of *H. bartholomaii* Flannery and Archer, 1987a, the condition may be an allometric effect because there is a considerable size difference between the two species. In this regard, it would be interesting to examine that region of the cranium of the Pleistocene giant musk-rat kangaroo, *Propleopus oscillans*.

In both macropodoid groups, the course of the frontoparetal suture is extremely variable and changes ontogenetically in conjunction with the gradual convergence of the frontal and temporal crests. Although the sutural figuration is not an entirely stalwart attribute, being ontogenetically and phyletically inconstant, the general trend is no less real. The top of the braincase, the entire frontal and nasal roof is missing. The small triangle of convergent parietals denotes the vertex of the cranium, and although the specimen is squashed, the integrity of its outline is preserved, leaving little doubt that the braincase was low and fairly broad. In macropodine kangaroos, the greatest breadth of the cranium is across the zygomatic arches, a considerable distance anterior to the glenoid fossa. In *Hadronomus* the greatest breadth of the cranium is significantly further back, at the level of the glenoid fossae. This imparts a triangular profile to the restored cranial outline (Figs 2C, 7B) and in this respect the cranial outline and its flat zygomatic arches is not unlike phalangerids and the primitive diprotodontoid *Ngapakaldia*.

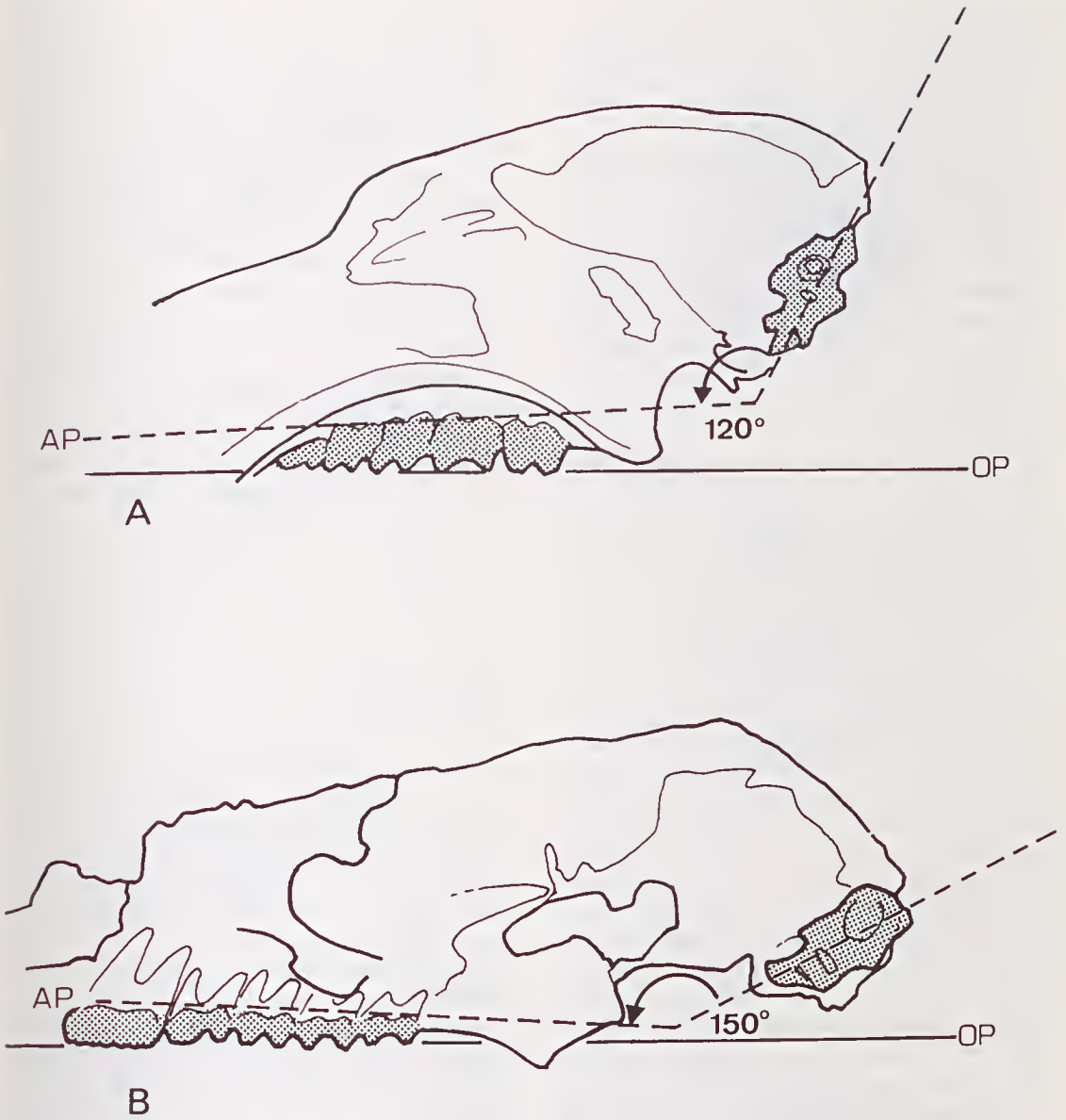**Cranial base.** The basicranial axis is represented by a nondescript fragment of pre-

Fig. 4. Comparison of the position and orientation of the petrosal in A, *Macropus robustus* and B, *Hadronomus puckridgi*, giving an indication of the difference in basicranial flexion between the two genera. Abbreviations: **OP**, occlusal plane; **AP**, alveolar plane, defined by the cemento-enamel junction. Note that A, *Macropus* is drawn from a sagittal section which illustrates the lingual side of the dentition whereas the buccal side of the cheektooth row is figured in B, *Hadronomus*.

sphenoid. The base of the neurocranial wing of the alisphenoid is present immediately anterior to the squamosal zygomatic process. The position of the anterior end of the pterygoid fossa is indicated by a bifurcation of the posteroinferior margin of the pterygopalatine process. A small portion of the alisphenoid is attached to the low, mesially wide maxillary postalveolar process. Both the palatine and pterygoid processes are

missing (Figs 1A,B, 7A). The basicranial axis and palatal plane is considerably less deflected than in *Macropus* (Fig. 4A,B). In the absence of the occipital condyles, the low angle of the cranial base in *Hadronomus* is indicated by the position of its petrous bone which lies scarcely above the occlusal line.

Orbit. The sutural contacts within the orbit are lost in a maze of cracks. The basic shape of the orbital fossa is slightly elliptical
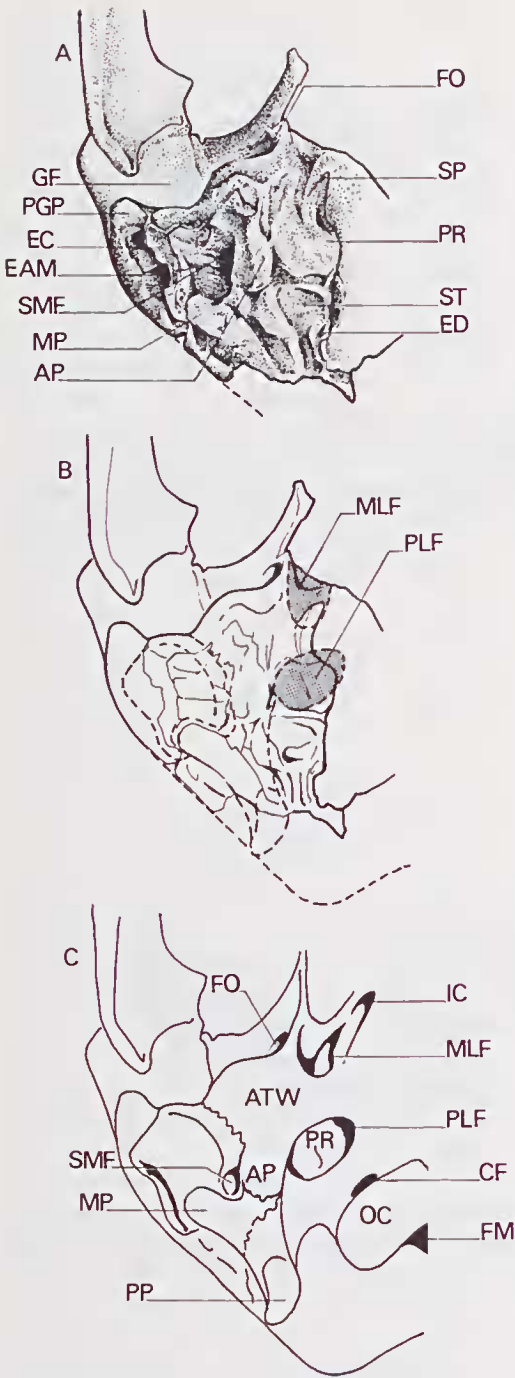
Fig. 5. Interpretation of the relations of the auditory region of the neurocranium of *Hadronomus*: A, poorly preserved surface anatomy of right side of the basicranium; B, approximate positions of the major landmarks sketched in; C, schematic interpretation of the structures. Abbreviations not previously defined: IC, internal carotid foramen; SP, superior process of the petrosal; PR, body of the petrosal; ST, sulcus representing the sigmoid portion of the transverse sinus; AP, alisphenoid portion of the paroccipital process; MP, mastoid portion of the paroccipital process; ED, endolymphatic duct; MLF, median lacerate foramen; PLF, posterior lacerate foramen; PP, paroccipital process; OC, occipital condyle; CF, condylar foramen; ATW, alisphenoid tympanic wing; FM, foramen magnum.

and perhaps relatively more elongated, smaller and deeper than in *Macropus* spp. The orbital margin of the jugal differs from macropodine kangaroos in being slanted mesially as opposed to being everted laterally. The lateral portion of the margin is thin and sharp in contrast to the wide, flattened emargination present in macropodines and sthenurines. Thin, sharp orbital margins are present in potoroid kangaroos. However, the orbital margin of *Hadronomus* appears to be trending towards the condition in *Macropus* with respect to its conspicuous mesial slant. If this trend were carried further, i.e. the jugal margin folding in on itself, a broad orbital emargination of the sort found in *Macropus* spp. would be the result. The lack of elaborate suborbital sculpturing in the jugal of *Hadronomus* accounts for the apparent lack of marginal eversion.

Auditory region. The superficial structures of the auditory region are scarcely represented and the remaining structures are badly damaged by large, wedge-shaped cracks. However, there is a sufficient representation of the middle ear region to elicit broad comparison with other macropodoids. In lateral aspect (Fig. 1A) the most obvious feature is the elongated, posteriorly slanted auditory arch occupied by a large, elliptical remnant of the ectotympanic. The ectotympanic is severely damaged, but it appears to have been anteroposteriorly attenuated and relatively large in diameter. The entire postsquamosal region, including a small remnant of the lambdoidal crest is slanted posteriorly in contrast to the nearly vertical relations of these structures about the external ear in *Macropus giganteus, M. rufa* and *M. robustus*. The ventral portion of the ectotympanic is comparatively thick and cancellous internally as in the sthenurine kangaroos. A ventral crest could have been present. Dorsally, the bone of the ectotympanic becomes very thin and may have been incomplete in its posterodorsal extremity. The opening of the ectotympanic tube (external auditory meatus) is less posteriorly directed and probably significantly shorter than in the large *Macropus* species (Fig. 5).
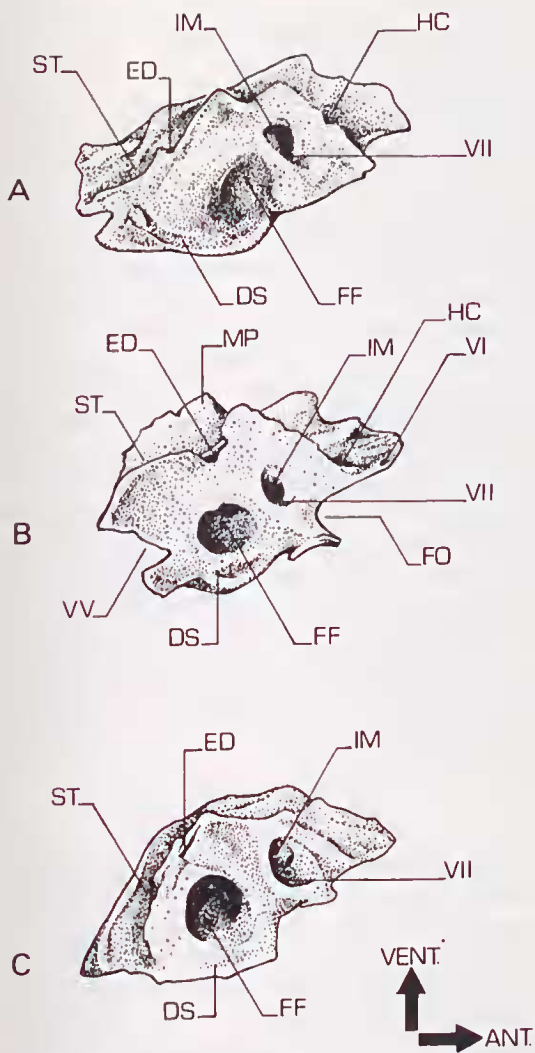
Fig. 6. Comparative morphology of the petrosal bones of A, *Hadronomus puckridgi*; B, *Macropus robustus*; C, *Potorous tridactylus*. Note the large, ovoid shallow floccular fossa FF in *Hadronomus*. Abbreviations: HC, canal hiatus of the facial nerve; IM, internal acoustic meatus; ED, endolymphatic duct; ST, sulcus for the sigmoid portion of the transverse sinus; VII, facial nerve canal; VV, posterodorsal notch of petrosal surrounding the anastomosis of the postglenoid and postzygomatic venous channels, the posterior extremity of which is damaged in *Hadronomus*.

The alisphenoid tympanic wing appears to have been broader and more inflated than in *Macropus* spp. Other macropodines, for example the Nail-tailed Wallaby, *Onychogalea unguifera*, have proportionally broad, inflated alisphenoid tympanic wings. Remnants of the mastoid and paroccipital processes are present on the specimen. Nei-

ther of these structures appear to differ in any particular way from the basic macropodoid morphology in which the alisphenoid and mastoid contribute flying buttress-like processes to the base of the paroccipital process. Judging from the thickness and steep angle of the break in the alisphenoid tympanic wing at the base of the paroccipital process, it is reasonable to assume that it contributed a substantial descending process, as in macropodids. The extensive broken basal portions of the process indicates that it was a robust structure, as large as that of *Macropus rufa*.

Immediately inferior to the ectotympanic, near the base of the paroccipital process there is a deep, vertically elliptical fossa which I have labelled as the stylomastoid fossa in Figs 1 and 3. It does not have the appearance of a breached paroccipital sinus, and appears to have a sulcus running anteroinferiorly from the opening, presumably for the facial nerve. In Fig. 5C, I have attempted to restore the overall relationships of the damaged superficial structures of the auditory region.

The ventral and internal surfaces of the well-preserved petrosal are exposed. The orientation of the petrosal of *Hadronomus* differs from that of *Macropus robustus* in being less inclined towards the vertical by about 30 degrees relative to the approximate horizontal plane of the toothrow (Fig. 4). The outline shape of the petrosal of *Hadronomus* is more elongated and narrower than in *Macropus robustus*, resembling more closely that of *Potorous tridactylus* (Fig. 6). The mastoid process of the periotic is much smaller and more horizontally oriented and the "jugular" process appears to be less prominent. As in potorids, the sulcus for the sigmoid portion of the transverse sinus is a distinct, broad channel with a fossa-like widening about midway along its course. In *Macropus robustus* it is a simple, trough-like groove. The ventral crest on the superior periotic process appears to have been thin and the medial surface of the process at the hiatus of the facial canal is smooth as opposed to rugose.

Although there are several more contrasts of a minor nature, I will mention only one more difference in the petrosal morphology which may be of some importance. In as many specimens of kangaroo petrosals as I have been able to examine, the floccular fossa

is very deep and undercut internally, behind its sharply defined orificial crest. *Hadronomus* has a large, oval, exceptionally shallow, floccular fossa with very rounded orificial margins (Fig. 6A). Although not as large in proportion to the body of the petrosal, the floccular fossa of *Hadronomus* resembles that of the hairy-nosed wombat, *Lasiorhinus latifrons* as much as it does any of the living kangaroo specimens used in this description.

The presence of a shallow floccular fossa (a "vombatiform" character) in *Wynyardia bassiana* was a primary argument by Archer (Archer 1984; Aplin and Archer 1987) against its having phalangeridan affinities, as postulated by Haight and Murray (1981). However, its value as a functionally related character has been overshadowed by its apparent systematic importance. The shallow floccular fossa is a direct reflection of the size and shape of the paraflocculus of the cerebellum. The flocculi are intimately related to the vestibular nuclei and their relative degree of development is closely associated with the extent to which balance and spatial orientation are important to the animal's locomotor repertoire (Sarnat and Netsky 1981). The flocculi are therefore greatly expanded laterally in agile arboreal species, such as primates and phalangeroid marsupials, flect bipedal cursors (kangaroos) and in lower vertebrate forms with well-developed lateral line systems. The flocculi are relatively reduced among slow-moving quadrupedal mammals and in general, among all terrestrial vertebrates (Sarnat and Netsky 1981).

The comparatively poorly developed flocculus of *Hadronomus* may be an indication that these were slow-moving kangaroos with a high degree of stability in their stance and gait. As speed and maneuverability are usually sacrificed for stability, it is likely that these were not specifically adapted to wide expanses of open habitat, as its name, "large wanderer" seems to imply. I have not been able to examine the floccular fossae of the petrosal of a sthenurine, but Tim Flannery (personal communication) informed me that they are also shallow.

Dentition. The crown morphology of *Hadronomus* is described in detail by Woodburne (1967). A few observations on the gross morphology of the cheek tooth row can be added to his assessment. Although the crowns of the upper molars lengthen progressively

from front to back, the total crown height (cementoenamel-junction to loph apex) decreases slightly from front to back. In macropodines, including protemnodonts, the crowns increase in height from front to back. Crown heights decrease from anterior to posterior in rat kangaroos (*Potorous, Hypsiprymnodon, Bettongia*) and, particularly $M_{3,5}$, in some sthenurines (see Tedford 1966, Fig. 3). The slanted implantation angles of the cheek teeth of *Hadronomus* are indicative of a high degree of mesial drift, an uncommon feature in potoroids, but characteristic of macropodine kangaroos. A feature present in the molar dentition of ASP889, to which I attach some significance further on, was not figured or described by Woodburne (1967). This is the formation of a cleft between the postparaconal crest and the formation of a cleft between the postparaconal crest and the buccal cingulum that resides on the labial margin of the interloph valley. The structure diminishes serially from M_2 to M_4 and is absent in M_5. In *Hadronomus* it is the site of the postparaconal wear facet described by Woodburne (1967).

DISCUSSION

The foregoing morphological description of *Hadronomus*, in which many of its features seem to be more comparable to those of potoroids than macropodids, might give the erroneous impression that the cranium of *Hadronomus puckridgi* resembles that of a potoroid. In fact, its overall appearance is that of a generalized macropodid, a bit protemnodont-like in lateral profile and somewhat sthenurine-like in specific features (Fig. 7). This is because the combined features normally used to phenetically discriminate macropodid from potoroid crania are really quite subtle and formally depend primarily on the character of the dentition and the possession in the latter, of a long, narrow, horizontal premaxilla.

As Woodburne (1967) observed, the cheek tooth morphology of *Hadronomus* is basically similar to that of the protemnodont macropodines and more specifically similar to that of the sthenurine kangaroos, especially in its possession of sharp, thin, evenly curved lophs and wide open, round-basined midvalleys with incipient mid-links. Sthenurine-like too, are the level, wide, though short and
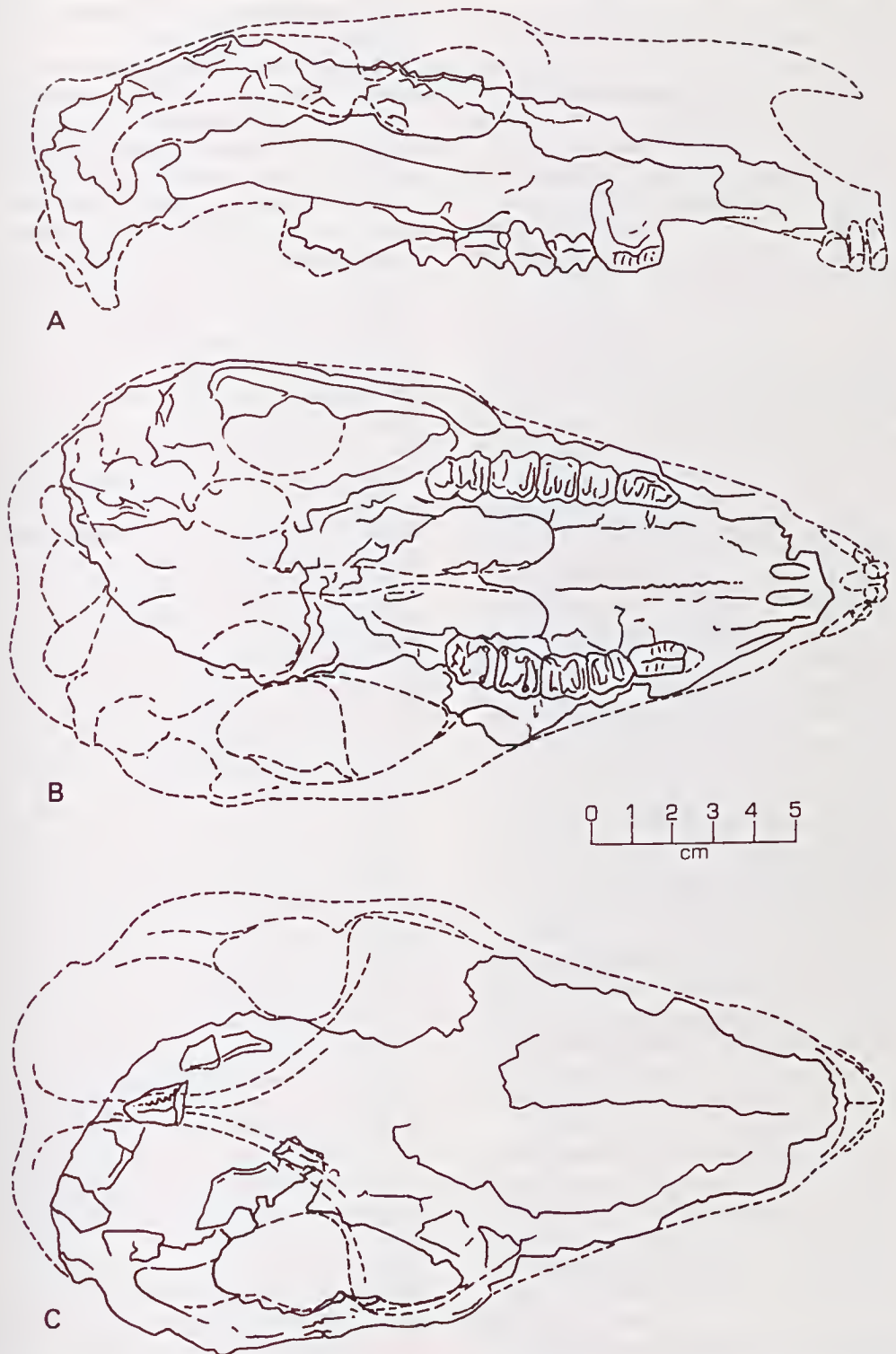
Fig. 7. Restoration of the cranium of *Hadronomus puckridgi* resulting in a lateral cranial profile reminiscent of *Protemnodon*: **A**, lateral aspect, note jugal morphology, low neurocranium; **B**, ventral aspect; showing invasive palatine vacuities and posteriorly broad cranial outline, relationship of the posterior portion of the jugal corrected to match lateral margin of the glenoid fossa. Profile of the nasals, alveolar portion of the premaxilla and the anterior frontal region is unknown; reconstruction is based on a minimal expression of features; **C**, dorsal aspect.

deep, shelf-like precingulae and enamel swellings along the buccal cusp bases.

The presence of a distinct labial link and distinct pre- and post-paraconal and metaconal crests are also suggestive of sthenurine molars. However, Sthenurines lack the conspicuous labial sulcus dividing the buccal crests in the interloph valley and the associated postparaconal and premetaconal facets apparently created by the rocking of the hypoconid at the end of each masticatory stroke.

The retention of prominent individual cusp points is a more subtle feature of *Hadronomus*'s molars. The individual cusps seem to become increasingly prominent as the lophs are reduced by wear. This trait is present to a far less extent in Sthenurines and not at all evident in *Protemnodon*. An analogous condition is present in the bilophodont molars of the folivorous colobine monkeys (Cercopithecidae) in which initial punctures by the prominent cusp points help to retain tension on the thin flexible leaf surface during the shearing process. They also initiate tearing of tough, thin vegetable matter by point-shearing (Walker and Murray 1968). *Hadronomus* is therefore a specialist folivore of some kind, my guess is that predominately they ate rather large, thin leaves as opposed small, thick, tough leaves such as *Acacia* phyllodes, which would require a component of crushing and less excursive, though more powerful shearing. This may be the basic difference functionally between the sthenurine dentition and that of *Hadronomus*.

The postparaconal and premetaconal facets seem to indicate that *Hadronomus* had a considerable axial rotation of its dentary during lateral excursion. This may explain the large lateral glenoid process which would have to accommodate a large rotational moment simultaneous with each side to side component of mastication.

The dentary, also previously described by Woodburne (1967) is practically unique among macropodoids for its exaggerated posterior depth, which however, is no greater than that seen in *Sthenurus brownei*. The dentary differs from the Sthenurinae principally in having a long, nearly horizontal symphysis, its relative thinness and in its flat medial and lateral surfaces. The diastemal crest abruptly terminates high above the alveolar sulcus of I_1 rather than tapering gradually towards the incisor root. It also lacks the

posterior mental foramen, a consistent synapomorphic feature of the Sthenurinae (Tedford 1966).

The dentition of *Hadronomus* is therefore similar enough to that of the sthenurines to allow for a possible ancestral relationship, although lacking any derived sthenurine features and being somewhat specialized functionally. Its molars appear to be less like those of protemnodont macropodines, although it is also possible to derive them from *Hadronomus*, as Woodburne (1967) observes.

Because the Sthenurinae appear to share a number of cranial synapomorphies with the macropodinae, including elevation of the cranial base high above the tooth row and detailed similarities in the zygomatic arch, orbit and prezygomatic portion of the maxilla (Tedford 1966) a direct ancestral relationship with the sthenurines seems unlikely. A direct cladistic connection with the protemnodont macropodines is however more remote due to the greater similarity of the dentition of *Hadronomus* to that of *Sthenurus*.

The plesiomorphic cranium of *Hadronomus* has relatively few unambiguously synapomorphic features in common with the Sthenurinae. In sthenurines, the jugal and maxilla are jointly produced forming a strong downward directed masseteric process. In *Hadronomus* the jugal is not involved. Like sthenurines, *Hadronomus* has large palatine vacuities and narrow palatine bars. It also has a thick, cancellous ectotympanic, as in the sthenurinae, but it is not known for sure whether it was long or ventrally keeled. Unlike sthenurines, the diastemal palatal surface does not appear to have been exceptionally short.

The most convincing similarities between *Hadronomus* and sthenurine crania are in the glenoid fossa morphology. The deep posterior jugal eminence, laterally expanded glenoid articular surface and the more lateral position and orientation of the postglenoid process form a possible constellation of synapomorphic features.

Hadronomus has a greater subjective resemblance with *Protemnodon* in cranial shape, which is elongated, low and broad posteriorly (Bartholomai 1973). However, the zygomatic arch morphology, degree of rostral decurvation, lack of palatal vacuities, deep suborbital shelf, long, delicate masseteric processes and the basically macropo-

dine features of the maxillary root, i.e. the sharply defined, long and oblique prezygomatic sulcus are all good macropodine synapomorphies that are conspicuously absent in *Hadronomus*. Consequently, I am reluctant to place *Hadronomus* in either subfamily as its cranial morphology seems to bear no closer relationship to one or the other. Moreover, the protemnodont macropodines and the sthenurines appear to be more closely related to one another with respect to cranial morphology than *Hadronomus* is to either. Indeed it has been suggested by Tedford (1966) that the sthenurines were derived from the macropodines. These similarities might be due to parallelism, but this possibility seems to be weakened by the radically different adaptive zones expressed in their respective morphologies.

This implies that another clade may be involved. With regard to systematics, *Hadronomus* can remain as macropodid Subfamily *Incertae Sedis*, assigned to one or another of the existing subfamilies (?Balbarinae, ?Macropodinae), placing considerable strain on their diagnoses, or its rank could be elevated to Subfamily status. Alternatively, the few ambiguous *Hadronomus-Sthenurus* synapomorphies, such as the glenoid fossa characters, could support an argument for its inclusion in the Sthenurinae, provided that the macropodine synapomorphies of sthenurines and macropodines are redefined as parallelisms or symplesiomorphic features as per Flannery (1983). However, *Hadronomus puckridgi* itself is geologically too late to be ancestral to these subfamilies. Both sthenurine and macropodine kangaroos appear to be present at Alcoota (Woodburne 1967).

The plesiomorphic cranium of *Hadronomus* emphasizes the uneasiness of the division between potoroid and macropodid kangaroos. The differences between the cranium of *Hadronomus* and certain potoroids are primarily a matter of degree. The cranial base of *Hadronomus* is not as low as in *Potorous tridactylus* or *Aepyprymnus rufescens* nor is it as elevated as the majority of macropodine and sthenurine kangaroos. The suborbital shelf, pterygoid fossae and basicranial relations of *Hadronomus* are proportionally similar to those of *Aepyprymnus* but embued with macropodid refinements such as the presence of an at least incipient auditory tube on the ectotympanic. On the other hand, the morphology of the petrosal appears to be very conservative.

Summary of Cranial Characters in *Hadronomus puckridgi*

Cranial base and Palate
1. Straight diastema and diastemal palate
2. Large confluent palatal vacuities
3. Straight basicranial axis, posterior neurocranium low
4. Shallow, posteriorly tapering suborbital shelf

Neurocranium
5. Parietal-alisphenoid sutural figuration
6. Acutely convergent parietofrontal sutures
7. Lambdoid crest overhangs occiput, low broad braincase

Zygomatic arches
8. Jugal straight, flat; anteorbital process long, broad
9. Jugal parallel-edged, not wedge-shaped
10. Low, shallow prezygomatic sulcus
11. Short, blunt crest-like masseteric process
12. Prominent lateral glenoid eminence and postglenoid process
13. small, elliptical orbital fossa with thin orbital margins
14. Long, nearly horizontal squamosal sulcus
15. Cranium widest across glenoid fossae
16. Lacrimal fossae large, extend anterior to orbit

Auditory region
17. Petrosal low, oriented at a very obtuse angle
18. Floccular fossa of petrosal large, shallow, oval
19. Mastoid petrosal process small, nearly horizontal
20. Auditory arch low, broad, posteriorly slanted
21. Large, broad, thick, cancellous ectotympanic
22. Alisphenoid tympanic wing broad, slightly inflated

Dentition
23. Long sectorial permanent premolar; lingual crest
24. Straight cheektooth row, low near equal-height crowns
25. Bilophodont, weak links, wide cingulae

26. Thin, trenchant curved lophs, thin enamel
27 Double crest in buccal interloph valley
28. Lack of enamel on lingual surface of I_1

Dentary
29. Posteriorly deep horizontal ramus
30. Steep alveolar boss above lower incisor root

Woodburne's (1967) systematic conclusions with regard to the derived sthenurines drawn from the tooth crown morphology of *Hadronomus* remain little modified by the additional information of the skull. *Hadronomus puckridgi* represents a primitive macropodid with certain characters that "anticipate" the derivation of the protemnodont macropodines and sthenurines. The cranium appears far less committed to either group than the macropodines and sthenurines are to each other. However, the possible synapomorphies between sthenurines and macropodines (large masseteric process, wide protolophid on M_1, lingual cingulum on P_3, reduced parastyle on M_1, loss of canine etc.) can all be attributed to parallel responses to a dietary shift from omnivory to browsing (Flannery 1983). It is therefore questionable as to whether the sthenurines are any closer to the macropodines than *Hadronomus*. One potentially useful feature of *Hadronomus* is the lack of an enamel coating on the lingual side of the crown of I_1, (Woodburne 1967) presumably a plesiomorphic condition, which clearly distinguishes it from the derived Sthenurinae. In sthenurines (except for *Lagostropheus*) the enamel is wrapped around the lingual surface (Flannery 1983).

Flannery (1983) regards *Lagostropheus* to be structurally the most primitive member of the Subfamily Sthenurinae based on a substantial inventory of synapomorphies. *Hadronomus* possesses no derived characters in common with *Lagostropheus,* that might be anticipated if the genus were directly ancestral to the Sthenurinae. Thus, as Flannery (1983) points out, while there are no specific features of *Hadronomus* that would rule out a relationship to the sthenurines, there are no convincing synapomorphic features to support its inclusion within the subfamily.

There can be little doubt that *Hadronomus* is a plesiomorphic representative of the basic macropodid clade from which the macropodines and sthenurines probably originated, but they appear to be too primitive cranially, too specialized dentally and too late geologically to be directly ancestral to either subfamily. Based upon current information, they appear to be the end of the line for a group of primitive macropodids that gave rise to no subsequent lineages.

The only other kangaroos presently known that may show a relationship to *Hadronomus* are the mid-Miocene Balbarinae and the Subfamily Indeterminate *Galanarla tessellata* (Flannery *et al.* 1982). Although much smaller, possessing dentaries of a much different shape and more primitive dentally, balbarines express a number of features in their lower dentitions that are vaguely suggestive of a possible shared ancestry with the late Miocene Alcoota genus.

There is a broad similarity in the simple low-crowned bilophodonty, proportions and shape of the lophs and relative (weak) development of the fore and midlinks, and bulbous crown-bases possessed by the two genera. However, balbarines have a distinctive M_2 morphology in which the trigonid is low and markedly narrow, the compression being due to the lingual offset of the protoconid (Flannery *et al.* 1982). In *Hadronomus* the protolophid is also constricted relative to the hypolophid, but the nature of the compression, by lingual migration of the protolophid, is not apparent, nor is the trigonid as narrow or low, relative to the talonid.

Balbarines retain a small paraconid on the lingual margin of the anterior cingulum of M_2. In *Hadronomus* a lingual emargination of the anterior cingulum results in an accentuated bulge of the cingulum in about the same position as the paraconid in *Balbaroo*, but to align these forms on the basis of such uncertain resemblances is like buying a lottery ticket. *Hadronomus* differs from *Balbaroo* in having a well-developed anterior cingulum and a poorly developed posterior cingulum. In *Balbaroo* the posterior cingulum of M_2 is prominent and broad (Flannery *et al.* 1982). The same area in *Hadronomus* is represented by a large bulge which protrudes out over the posterior root of the hypolophid in lateral view (Woodburne 1967). Moreover, the lophs of *Balbaroo* are stouter, less tapered towards their apices, the enamel is relatively thicker and the buccal cingulum is broadly continuous across the midvalley. If *Hadronomus* were directly related to *Balbaroo,* some of

these very distinctive features should be in evidence.

The lower molars of *Galanarla tessellata* show a closer overall resemblance to those of *Hadronomus*, particularly in the proportions of the lophs, development and shape of the anterior cingulae, broad interloph valleys and less prominent buccal cingulum. The lower incisor alveolus on the dentary is distinctively stepped above the emergence of the root as in *Hadronomus*, and the I_1 is long-rooted, straight, lanceolate-crowned and lacks enamel on the lingual side. However, like *Balbaroo*, *Galanarla* has a large, distinct posterior cingulum.

The unassigned upper molars (Fig. 8E-F in Flannery *et al.* 1982) differ from *Hadronomus* in having a slight sinuosity of the lophs, relatively lower lophs and shorter, narrower anterior cingulae. They otherwise share the distinctive double crest which blocks the labial side of the interloph valley, a wide interloph valley and the presence of a post-link. The unassigned macropodid upper molars could have given rise to *Hadronomus* by slight suppression of the post-link and with a slight reduction of the width of the labial sulcus dividing the postparaconal crest and the buccal cingulum.

CONCLUSIONS

Although inconclusive, these various similarities tend to align *Hadronomus* with the more archaic macropodids; implying that the subfamilially unassigned mid-Miocene macropodid taxa, *Galanarla* and gen. et sp. unnamed (Flannery *et al.* 1982:229) are more closely related to *Hadronomus* than *Hadronomus* is to the sthenurines. The balbarines are generally similar but have no synapomorphies with *Hadronomus*. *Galanarla* is somewhat more sthenurine-like in having a curved molar row (macropodines tend to have fairly straight or excurvate lower molar rows), but with its distinctly potoroid-like offset of the premolar roots, a direct relationship is highly unlikely.

As there are no crania assigned to these forms, the wider systematic observations made here do not result from the primary consideration of this paper. However, the cranium of *Hadronomus* on its own has demonstrated that the genus is no closer to sthenurines than its dentition indicates, indeed it

strongly reinforces the long-standing reservations about its relationship to any of the derived macropodids expressed originally by Woodburne (1967) and subsequently by Flannery (1983). Consequently, it has been concluded that *Hadronomus* is a representative of a distinct group of primitive macropodids that became extinct at the end of the Miocene.

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